

Response in Nematocyst Uptake by the Nudibranch *Flabellina verrucosa* to the Presence of Various Predators in the Southern Gulf of Maine

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Abstract. Aeolid nudibranchs maintain nematocysts sequestered from their cnidarian prey for protection against predators. Selection for nematocyst incorporation is a function of diet and prey choice, but ratios vary among nudibranchs feeding on a given diet, indicating that other factors may be involved. It is proposed that the presence of predators influences nematocyst incorporation. Nematocyst uptake in the nudibranch *Flabellina verrucosa* collected from the southern Gulf of Maine was examined in response to various potential predators, including *Crossaster papposus*, *Tautogolabrus adspersus*, and *Carcinus maenas*. Nudibranchs in individual flow-through containers feeding on a diet of the hydroids *Tubularia* spp. and *Obelia geniculata* were subjected to tanks containing a predator, then their nematocyst distribution was examined. Although most of the changes over the experimental period were attributable to diet, *F. verrucosa* responded to both *T. adspersus* and *C. papposus* by significantly increasing microbasic mastigophore incorporation. No differential uptake was seen with *C. maenas*. Response was evident in the nudibranchs both for predators present in the collection area and for those with which they had no previous exposure, indicating that *F. verrucosa* modulates nematocyst incorporation in response to the presence of predators as well as to diet. A coevolution of nudibranchs and potential predators may govern changes in nematocyst uptake.

Introduction

Prey anti-predator responses are crucial to prey survival, though studies of predator-prey coexistence often focus on predator characteristics (for reviews see Murdoch and Oaten, 1975; Hassell, 1978; Taylor, 1984). Prey species reduce their mortality from predation by using a variety of tactics. Mobile animals may be protected by armored or cryptic morphologies, noxious chemicals, and a variety of escape behaviors (Edmunds, 1974; Pianka, 1983; Havel, 1987). In marine communities, opisthobranch nudibranchs would seem a likely prey item since they are not protected against predation by the shell employed by prosobranch gastropods. To compensate for the lack of a natural physical refuge, nudibranchs have developed various defensive strategies, including avoidance behaviors, cryptic or aposematic coloration, spicules, toxic secretions, and stinging nematocysts (summarized by Harris, 1973). They are slow-moving and often flamboyantly colored or on contrasting substrate, but despite their being seemingly easy prey, there are few reports of predation on nudibranchs (Thompson, 1976; Karuso, 1987; Faulkner, 1992; Proksch, 1994), thus demonstrating the efficacy of nudibranch defense tactics.

An aspect of predator-prey interactions unique to the defensive strategies of some aeolid nudibranchs is their use of cnidarian nematocysts. For armament against predators, these nudibranchs maintain an arsenal of functional stinging nematocysts that they acquire, through ingestion, from their cnidarian prey (Thompson, 1960; Edmunds, 1966; Thompson and Bennett, 1969; Greenwood and Mariscal, 1984a, b). Nematocysts pass through the digestive tract to the tips of the dorsal cerata, where they are incorporated into specialized cavities called cnidosacs and are maintained in a functional state (Conklin and Mariscal, 1977; Greenwood and

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Abbreviations: BI, basitrichous isorhizas; DS, desmosomes; HeA, heterotrichous anisorhizas; HI, holotrichous isorhizas; HME, heterotrichous microbasic euryteles; HoA, holotrichous anisorhizas; MA, microbasic amastigophores; MM, microbasic mastigophores; ST, stenoteles.

Mariscal, 1984a). The nematocysts are then available to be ejected by the nudibranch, presumably as a defense mechanism.

While it is well understood that aeolid nudibranchs store cnidarian nematocysts from their prey, the dynamics of nematocyst selection are not explicit. There are more than 25 types of nematocysts in cnidarians (see Mariscal, 1974), each with different functions in prey acquisition and defense, and those present in a given cnidarian are a function of the species. Therefore, specific nematocysts are present in varying combinations and proportions among nudibranch prey species (Mariscal, 1974; Calder, 1988). Nudibranch nematocyst incorporation is a function of availability in the diet, so depending on the cnidarian prey they consume and on which parts of the prey, nudibranchs sequester different kinds of nematocysts within their cnidosacs. Additionally, they can preferentially select specific types from what is available (Grosvenor, 1903; Day and Harris, 1978). The nematocyst complement serves as a measure of feeding history, as nudibranchs incorporate a small number of all nematocyst types found in the prey they have been consuming. However, individuals of a given nudibranch species feeding on the same diet sequester varying proportions of those nematocyst types (pers. obs.), indicating that factors other than strict availability must be involved in selection.

Predation pressure may influence nematocyst uptake, and therefore different nematocyst types may be selected in response to specific predators. Since nudibranch nematocysts purportedly function as predator deterrents, predator cues may affect nematocyst incorporation such that nudibranchs maintain weapons capable of combating predators specific to the area in which they live. Edmunds (1966) suggested that certain nematocyst types may be more effective against some predators—penetrants for use against fish and adherents against crustaceans, for example—so nematocyst incorporation may be based on nudibranch predators in the vicinity. Despite studies of individual species populations, few studies have examined variation with respect to the predation pressure encountered by the organism in question. The objective of this study was to identify changes in nematocyst uptake by nudibranchs in response to chemical cues from potential predators. My work examines the incorporation of nematocysts by nudibranchs in response to individual predator species and considers both predation pressure and the nudibranch's previous experience. To further elucidate the relationship between nematocysts in nudibranch cnidosacs and predation pressures, I examined nematocyst uptake in the nudibranch *Flabellina verrucosa* with and without exposure to potential predators. I hypothesize that (a) the presence of specific predators differentially affects nematocyst uptake, (b) response depends on the nudibranch's previous exposure to the predator, and (c) response depends on the predator's ability to prey on the nudibranch. By testing these hypotheses I will determine

whether population-level variation in nematocysts sequestered by *F. verrucosa* provides a link between nematocyst incorporation and predation pressure.

Materials and Methods

Study organisms

Flabellina (formerly *Coryphella*) *verrucosa* (= *rufibranchialis*) (Sars, 1829) is a common aeolid nudibranch in the shallow marine subtidal throughout the Gulf of Maine. Its distribution is circumboreal: in the Atlantic its range includes northern Europe (British Isles, Norway, and Iceland) and Greenland south to the Gulf of Maine; in the Pacific *F. verrucosa* can be found off British Columbia and the coast of Russia (Bleakney, 1996). A generalist predator, *F. verrucosa* consumes numerous athecate hydroid species, scyphistomae, and tunicates (Kuzirian, 1979). No predators are known to prey primarily on this nudibranch.

In the following experiments, *F. verrucosa* was exposed to a variety of predators, and nematocyst uptake was compared with uptake in the absence of predator cues. The predators to which *F. verrucosa* was exposed included the wrasse *Tautoglabrus adspersus* (Walbaum, 1792), the sea star *Crossaster papposus* (Linnaeus, 1767), and the green crab *Carcinus maenas* (Linnaeus, 1758). *Crossaster papposus* is present in cold deep waters in the southern Gulf of Maine collection area, though none were observed at the depths where nudibranchs were collected for this study. While not a nudibranch specialist, *C. papposus* feeds on nudibranchs, including *F. verrucosa*, when they are encountered in the field (Mauzey *et al.*, 1968) (pers. obs.). Among its other prey, the wrasse *T. adspersus* (cunner) is known to feed voraciously on some nudibranch species, but shows an aversion to consuming *F. verrucosa* (Harris, 1986; pers. obs.). Cunner are seasonally abundant in the southern Gulf of Maine in the summer and fall when water temperatures are mild, but they are absent during the colder winter and spring seasons. The omnivorous green crab *Carcinus maenas* is common both intertidally and subtidally throughout the Gulf of Maine, but unlike some crab species reported to prey on certain nudibranchs (Harris, 1970; Ajeska, 1971), *C. maenas* is not a known nudibranch predator.

The experience that specimens of *F. verrucosa* collected in the southern Gulf of Maine have had with the predators used in this study ranges from common exposure (*C. maenas* and *T. adspersus*) to no probable exposure (*C. papposus*) for nudibranchs of the collected generation. Depending on collection location, there may be differences in exposure to cunner: nudibranchs collected from mooring chains at Shoals are less likely to have encountered *T. adspersus* than those from Nubble (description below). At Nubble, fish forage and live on the wall where nudibranchs were collected, but at Shoals, the mooring lines do not support substantial populations of the predatory fish. For all collec-

tion sites, nudibranchs are unlikely to be found deep enough to have been exposed to *C. papposus* prior to collection. However, parental generations of *F. verrucosa* may have been exposed to the entire suite of experimental predators in other areas within the species' range, presenting the possibility that nematocyst uptake could be influenced by a coevolutionary response based on exposure of previous generations to the predators used in this study.

Specimen collection

Nudibranchs were collected from two locations within the southern Gulf of Maine: Cape Neddick (Nubble) in York, Maine (43°9'54"N, 70°35'29"W), and Gosport Harbor near Appledore and Lunging Islands of the Isles of Shoals island group located about 10 km off the coast of New Hampshire (42°59'21"N, 70°36'54"W). The shallow subtidal of Cape Neddick and the Isles of Shoals are both algal-dominated, gradual slopes containing vertical rock surfaces and undercuts dominated by animal communities. Nudibranch populations at these sites are of the same genetic stock due to site proximity and widespread dispersal of planktonic veliger larvae, but their post-settlement feeding histories may differ due to the availability of prey items at the two locations.

Between 30 and 50 specimens of *Flabellina verrucosa* were collected from vertical rock wall surfaces at Nubble in 3–8 m of water, and also from blooms of the hydroid *Tubularia crocea* on mooring ball lines near the Isles of Shoals (Appledore and Lunging Islands) in October and November 2001 and January 2002. Animals were maintained following collection and for the duration of all experiments at 10 °C in a constant-temperature room at the University of New Hampshire. Tanks were filled with natural seawater obtained from the Coastal Marine Laboratory at the Portsmouth Coast Guard Station at the mouth of Portsmouth Harbor (43°4'20"N, 70°42'37"W). Animals for each site were kept together and used separately in each experiment.

Experimental setup

Experimental tanks containing a predator were established 1–2 days before experiment inception. Control tanks did not contain a predator. Following initial nematocyst counts (procedure described below) for each nudibranch population, nudibranchs were placed in individual flow-through containers with two hydroid food sources. The hydroids used were *Obelia geniculata* (Linnaeus, 1758) and *Tubularia* spp. (*crocea* and/or *indivisa*), each present in excess so that food was not a limiting factor. Examination of the tissues of these cnidarian prey species revealed mutually exclusive nematocyst complements (Table 1), so they offer a variety of nematocyst types. *Tubularia* spp. were collected from the nudibranch collection sites at the Isles of Shoals,

Table 1

Nematocyst types found upon examination of cnidarian prey tissues

Hydroid species	Nematocysts apparent in tissue*
<i>Obelia geniculata</i>	MM, MA
<i>Tubularia indivisa</i> , <i>T. crocea</i>	ST, DS, HeA, HME, BI

* Nematocyst types are abbreviated as follows: MM, microbasic mastigophores; MA, microbasic amastigophores; ST, stenoteles; DS, desmonemes; HeA, heterotrichous anisorhizas; HME, heterotrichous microbasic euryteles; BI, basitrichous isorhizas.

and *O. geniculata* from pilings at the Portsmouth Coast Guard Station. The hydroids used as prey were not fed during the experiment and have no direct ecological relationships with the predators used in the study.

Experimental flow-through containers remained in the tanks for 2 weeks, with a fresh replacement of hydroid food and a partial water change in the tanks after 7 days. Control tanks had five containers for each nudibranch population randomly distributed among the tanks. After 2 weeks of exposure to the experimental conditions, the nematocyst content of each nudibranch was evaluated by examining ceras squashes for three cerata per animal *via* light microscopy. Cerata were removed from the anterior region in the first or second ceratal cluster by using forceps combined with the animals' propensity to autotomize these projections. For each ceras, 100 nematocysts (identification according to Mariscal, 1974; see reference for visual representations) were categorized on the basis of visual characteristics (if the field of view included more than 100 nematocysts, all in the field were counted). Counts included both fired and encapsulated (unfired) nematocysts. The setup was repeated with each predator and for each nudibranch collection site, adjusted as described below. The numbers of replicates for each experiment are summarized in Table 2.

For the *C. papposus* experiment, ten 2.5-gallon tanks containing a sea star measuring 2.7–6.5 cm and three 2.5-gallon tanks without a sea star were established. Each tank contained one container for each nudibranch collection site. The sea stars were starved for the duration of the experiment because they refused to eat regularly once brought into the laboratory. The experiment using the cunner *T. adspersus* was conducted similarly, but due to limited numbers of captive fish, it involved six 10-gallon tanks, each containing two flow-through containers for each experimental site. The cunner in the tanks measured between 7 and 17 cm and were fed locally collected *Mytilus edulis* meat every other day. When the green crab *Carcinus maenas* was used as the predator, tank setup and size was equivalent to that used for the *C. papposus* experiment, with crab carapace size ranging from 5.5 to 7.0 cm. Crabs were fed frozen cooked

Table 2

Summary of experimental design, including number of replicate flow-through containers for each population and each treatment

Predator treatment	Number of experimental containers	Number of experimental tanks	Number of control containers	Number of control tanks
<i>Crossaster papposus</i>	10	10	5	3
<i>Tautoglabrus adspersus</i>	12	6	6	3
<i>Carcinus maenas</i>	10	10	5	4

shrimp two to three times weekly for the duration of the experiment.

Total numbers of nematocysts for each condition were analyzed using chi-square tests of independence to identify differences in the distribution of nematocysts. Pairwise ANOVA analyses were performed on average nematocyst proportions for each nudibranch using the PC program Systat 9.0 to determine the nematocyst types that were exhibiting changes for each comparison of conditions.

Results

Southern Gulf of Maine populations of *Flabellina verrucosa* responded to the presence of some experimental predators by changing which nematocyst types they incorporated. Field-collected nudibranchs showed a wide range of incorporated nematocysts and high variability between individuals and between sites (Fig. 1), with stenoteles (ST), desmonemes (DS), and heterotrichous microbasic euryteles (HME) sharing dominant percentages. The results for predator exposure are subdivided below, and nematocyst incorporation response for all predators is summarized in Table 3. All results marked as being significant are based on *P* values less than 0.05.

Southern Gulf of Maine predator responses

Flabellina verrucosa responded to the presence of *Crossaster papposus* with significantly increased incorporation of microbasic mastigophores (MM) and depressed uptake of heterotrichous anisorhizas (HeA) (Fig. 2A). In response to *Tautoglabrus adspersus* (cunner), incorporation of MM was also significantly increased (Fig. 2B), while uptake of heterotrichous microbasic euryteles (HME) and stenoteles (ST) was depressed. The presence of the green crab *Carcinus maenas* evoked no significant differences in nematocyst incorporation compared to control nudibranchs (Fig. 2C); all differences were attributable only to change due to the provided diet.

Site-dependent responses

Trends in nematocyst incorporation depended on the predator used, not the site where the nudibranchs were

collected. However, these trends were not always significant.

When exposed to the sea star *Crossaster papposus*, nudibranchs from Shoals significantly adjusted their nematocyst incorporation, (Fig. 3A) following the same trends as the combined data for the two sites (Fig. 2). Those from Nubble showed no significant differences attributable to the presence of *C. papposus*, but showed a propensity for increased incorporation of MM (Fig. 3B).

Exposure to the cunner *T. adspersus* also triggered significantly increased incorporation of MM in the Shoals population when compared to the control group (Fig. 4A), while uptake of three other nematocyst types was depressed. Nudibranchs from Nubble showed similar trends of increasing nematocyst incorporation, but the only significant difference was lower uptake of microbasic amastigophores (MA) in the experimental nudibranchs (Fig. 4B).

As in the combined test (see Fig. 2C), the presence of *Carcinus maenas* did not elicit differences in nematocyst incorporation for experimental nudibranchs in comparison with control animals for either the Shoals or Nubble populations.

Control comparison

Individual southern Gulf of Maine populations incorporated nematocysts similarly from the provided hydroid diets, yet exhibited some differences in nematocyst uptake in the absence of predator cues. However, results were not consistent between experiments when comparing control groups from the different collection sites (Fig. 5). In the experiment with *C. papposus*, nudibranchs collected from Shoals had significantly higher incorporation of ST (Fig. 5A). In the *T. adspersus* experiment, Nubble nudibranchs retained a significantly higher percentage of desmonemes (DS) than the Shoals population, and significantly fewer HME and holotrichous anisorhizas (HoA) (Fig. 5B). Conversely, the control comparison from the *Carcinus maenas* experiment showed that nudibranchs from Shoals kept more DS (Fig. 5C).

Discussion

The animal world offers numerous illustrations of predator incorporation of prey defense mechanisms. Some of the

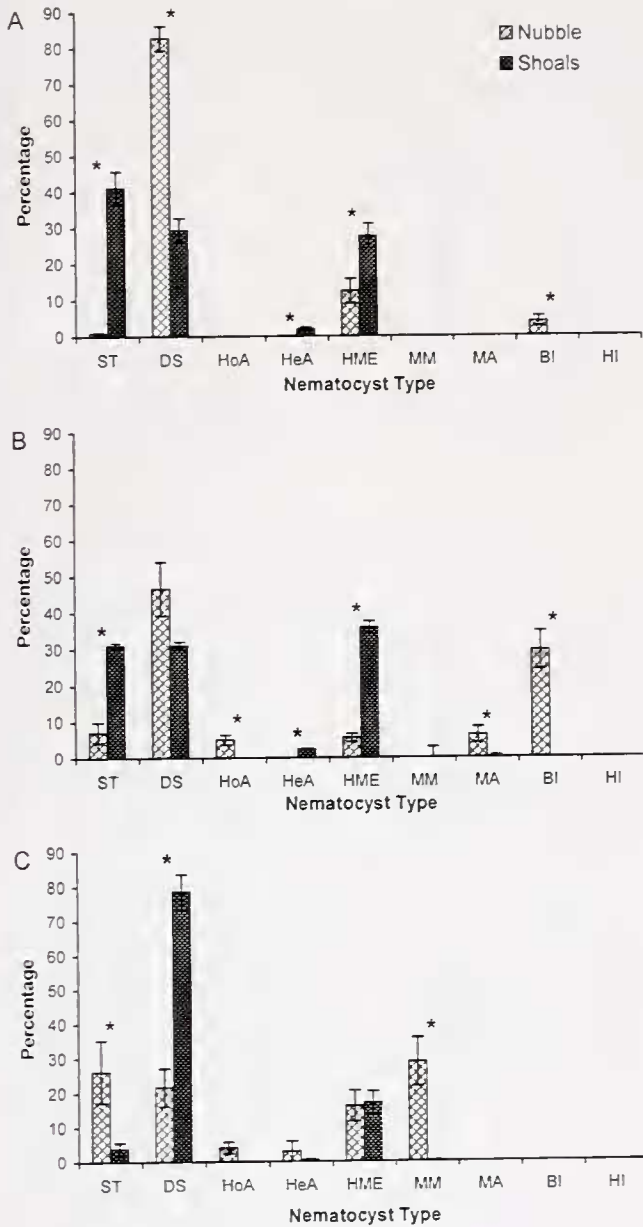


Figure 1. Initial distribution of nematocyst types in *Flabellina verrucosa* collected from two sites in the southern Gulf of Maine. Results are presented according to the predator experiment for which the nudibranchs were collected: (A) *Crossaster papposus*, (B) *Tautogolabrus adspersus*, and (C) *Carcinus maenas*. *Indicates significant differences. $P < 0.05$. Nematocyst types: ST, stenoteles; DS, desmosomes; HoA, holotrichous anisorhizas; HeA, heterotrichous anisorhizas; HME, heterotrichous microbasic euryteles; MM, microbasic mastigophores; MA, microbasic amastigophores; BI, basitrichous isorhizas; HI, holotrichous isorhizas.

most specialized species store prey-derived toxins and use them for their own chemical defenses against predators at the third trophic level (Rowell-Rahier and Pasteels, 1992). Among the many examples in insects and vascular plants (Rothschild, 1973; Rowell-Rahier and Pasteels, 1992), the most famous involves monarch butterflies utilizing carde-

nolides from milkweed host plants (Brower *et al.*, 1972, 1975; Brower and Moffitt, 1974; Dixon *et al.*, 1978; Calvert *et al.*, 1979; Seiber *et al.*, 1986; Malcolm and Brower, 1989; Malcolm and Zalucki, 1996). In the marine realm, some dorid nudibranchs sequester chemical compounds from sponges for defense against predators (Karuso, 1987; Scheuer, 1990; Faulkner, 1992; Proksch, 1994). With both monarch butterflies and dorid nudibranchs, the uptake process is selective in that the predator incorporates specific compounds from those available in the host (monarchs: Seiber *et al.*, 1986; nudibranchs: Proksch, 1994). However, while the process is discriminatory, there is no evidence that selectivity can be modified in response to environmental cues. In the case of *Flabellina verrucosa* and its incorporation of cnidarian nematocysts, the animal not only has choices as to the specific defensive structure to sequester, but as shown in this study, the selection can also be based on chemical cues from specific predators. This is an instance of secondary induction, where the nudibranch responds to the presence of predators by altering incorporation of defensive organelles from the cnidarian prey.

Flabellina verrucosa from the southern Gulf of Maine responded to both *Crossaster papposus* and *Tautogolabrus adspersus* by increasing incorporation of one type of penetrating nematocyst, the microbasic mastigophore. In cnidarians, this nematocyst has been suggested to be an effective defense against predation by the nudibranch *Cratena pilata* (Kepner, 1943); when incorporated by a nudibranch, it may also be effective against a diverse suite of predators. For nudibranchs, as for cnidarians, use of a single type of nematocyst against many predators may be more efficient than needing a different nematocyst for each potential predator.

Given the experimental nudibranchs' lack of field exposure to some of the predators used in this study, the uptake of a single nematocyst type (MM) in response to multiple predators could reflect an inducible defensive selectivity. Such selectivity may be attributable to a variety of factors, including the long-term coevolution of nudibranchs with these predators, genetic control over nematocyst response to predator cues, or a propensity to take up a particularly noxious nematocyst when any potential predators are present. The ability of *F. verrucosa* to respond to *C. papposus* and *T. adspersus* can be explained in two ways: either nudibranchs in this generation have had prior experience with these predators, or they are demonstrating a coevolutionary response based on exposure to these predators over time. Individuals of *F. verrucosa* collected from the southern Gulf of Maine are likely to have been exposed to *T. adspersus*, and they responded strongly by increasing uptake of a potent nematocyst (Fig. 2B). Nudibranchs from the two collection sites showed the same trends when exposed to cunner, but the response was not significant for the specimens from Nubble (Fig. 4, Table 3). The ecological

Table 3

Significant change in nematocyst incorporation between experimental and control *Flabellina verrucosa* when exposed to each predator for each individual collection site and the combined southern Gulf of Maine

Population	Significant changes in nematocyst incorporation	Predator		
		<i>Crossaster papposus</i>	<i>Tautoglabrus adspersus</i>	<i>Carcinus maenas</i>
Combined southern Gulf of Maine	Increased	MM ($P = 0.004$)	MM ($P = 0.001$)	(NR)
	Decreased	HeA ($P = 0.006$)	HME ($P = 0.033$), ST ($P = 0.003$)	(NR)
Nubble	Increased	(NR)	(NR)	(NR)
	Decreased	(NR)	MA ($P = 0.009$)	(NR)
Shoals	Increased	MM ($P = 0.038$)	MM ($P = 0.000$)	(NR)
	Decreased	HeA ($P = 0.003$)	HME ($P = 0.000$), ST ($P = 0.000$), HeA ($P = 0.047$)	(NR)

Nematocyst types are abbreviated as follows: MM, microbasic mastigophores; HeA, heterotrichous anisorhizas; HME, heterotrichous microbasic euryteles; ST, stenoteles; MA, microbasic amastigophores. (NR) indicates no significant response.

context of nudibranchs and cunner at this site may explain the lack of significance: although the nudibranchs settle among a dense population of cunner and may be nipped at, they may recognize that these fish do not represent a valid threat; thus they are less likely to significantly change their incorporation of nematocysts. However, the nudibranchs used in this study are unlikely to have encountered *C. papposus* at the shallow subtidal sites where they were collected, yet they still modified their nematocyst incorporation (Fig. 2A). By increasing incorporation of a formidable penetrant, specimens of *F. verrucosa* are probably demonstrating a response due to their long-term coevolution with both experimental predators in other parts of their circumboreal distribution. In this study, regardless of the likelihood of previous individual exposure to the potential predator, *F. verrucosa* countered by incorporating larger percentages of the penetrating microbasic mastigophore.

Conversely, *Carcinus maenas* is a common crab in the Gulf of Maine and also co-occurs with *F. verrucosa* in Europe, but it is not known to actually prey upon *F. verrucosa*. Therefore, the nudibranch's failure to modify the type of nematocysts it sequesters when exposed to chemical cues from the green crab is not surprising. Thus, incorporation of specific nematocyst types is increased in response only to realistic potential predators and can be modified depending on the specific predator cue the nudibranch receives.

This system is unique in that nudibranchs selectively incorporate the defenses of another organism for specialized adapted defense against their predators. The indirect interactions in the system are analogous to trait-mediated indirect effects. Such effects arise when one species modifies the way two other species interact by causing changes in the behavior of the intervening species (Abrams, 1995; Abrams *et al.*, 1996; Werner and Anholt, 1996; Schmitz and Suttle, 2001). In interactions involving *Flabellina verrucosa*, the presence of a predator elicits a response from the nudibranch, but the cascade continues down the food web to the

level of the nudibranch's cnidarian prey. Responses to increased predation that result in changes in prey use are examples of trait-mediated indirect effects (*e.g.*, Messina, 1981; Power *et al.*, 1985; Turner and Mittelbach, 1990; Huang and Sih, 1991; McIntosh and Townsend, 1996; Peacor and Werner, 1997; Beckerman *et al.*, 1997; Turner *et al.*, 1999). *Flabellina verrucosa*'s increased incorporation of microbasic mastigophores from its cnidarian prey in the presence of the predators *Crossaster papposus* and *Tautoglabrus adspersus* is a unique example of such an interaction.

The hydroid species used in this study were abundant at both collection sites. *Flabellina verrucosa* is more often found associated with the *Tubularia* spp. (pers. obs.), though the nudibranchs collected had nematocysts representative of both experimental prey species (Fig. 1). However, the trends in preferential uptake of specific nematocysts shown between nudibranch populations collected from different sites and substrates may be related to pre-collection feeding differences. In addition to post-experimental changes in nematocyst uptake in response to the presence of some predators, the populations considered here incorporated somewhat different nematocysts from the provided diet even when no predator was present, as seen in the control comparisons (see Fig. 5).

The differences observed may demonstrate acquired tendencies of incorporation as a result of feeding history or disparities in the populations' ingestive conditioning. Ingestive conditioning affects selection of prey species in other aeolids such that they will preferentially prey upon species they have been feeding upon recently (Hall *et al.*, 1982; Hall and Todd, 1984), but it has never been considered with respect to nematocyst selection. However, all nematocyst types that were significantly different in the control populations at the end of the experiment (Fig. 5) had also been significantly different when the nudibranchs were collected (Fig. 1). The original nematocyst complement may still

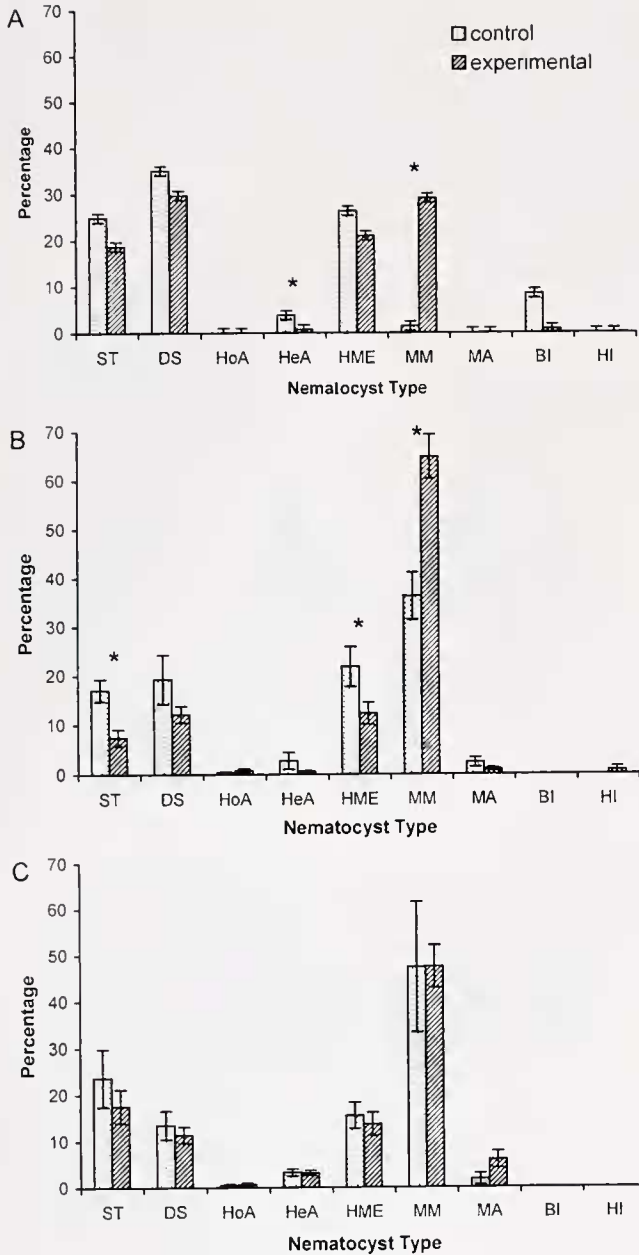


Figure 2. Changes in nematocyst uptake by *Flabellina verrucosa* collected in the southern Gulf of Maine in response to predator cues: (A) *Crossaster papposus*, (B) *Tautoglabrus adspersus*, (C) *Carcinus maenas*. *Indicates significant differences, $P < 0.05$. Nematocyst types as in Figure 1.

have been affecting the cnidom, though nematocysts in *F. verrucosa* are replaced quickly, with complete exchanges occurring within 12 days of switching diets (Day and Harris, 1978). These results indicate that ingestive conditioning may play a role in nematocyst preference in subsequent feeding trials, though directed responses to predator cues are possible despite such tendencies.

Preferential feeding on *Obelia geniculata* by *F. verrucosa* in the presence of *T. adspersus* and *C. papposus* could

explain the observed increase in MM, as *O. geniculata* is the source of this nematocyst type for the experiment. However, nematocysts from the *Tubularia* spp. tissue (ST, DS, and HME) were also present at high levels in these animals. Although nudibranch feeding preference was not quantified, when the experiments were monitored or cnidarian prey were changed, nudibranchs were observed more often on the *Tubularia* hydroids. This observation and the presence of tubularian nematocysts suggest that a superficial preference for consuming *O. geniculata* in the face of predators cannot solely explain the increase in microbasic mastigophores.

The ability of a prey species to react by optimizing specific defense mechanisms against a given predator increases its fitness by decreasing mortality by predation. While this study has not shown any particular nematocyst to be an effective weapon against a specific predator, the nudibranchs' change in nematocyst selectivity suggests a directed response in which choices about prey use and nematocyst incorporation are made in response to predator cues. However, work on the specifics of that response and on its effectiveness against the predators is still lacking.

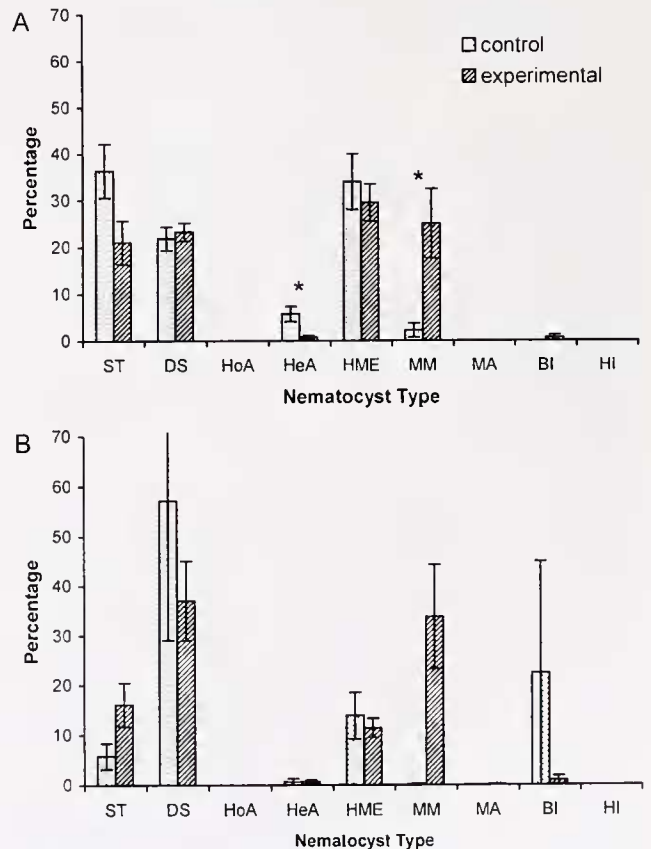


Figure 3. Site-dependent responses in nematocyst uptake by *Flabellina verrucosa* caused by cues from *Crossaster papposus* for nudibranchs collected from (A) Isles of Shoals and (B) Nubble. *Indicates significant differences, $P < 0.05$. Nematocyst types as in Figure 1.

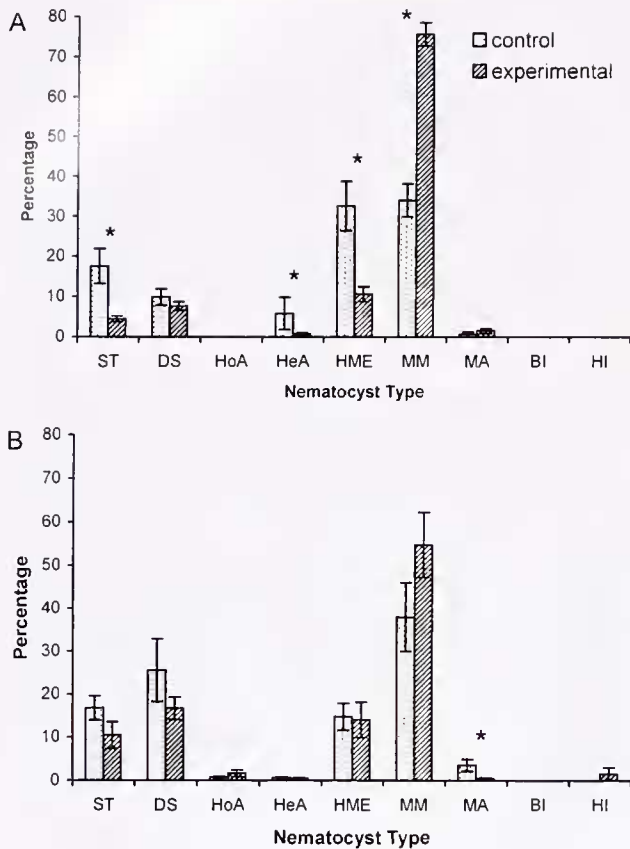


Figure 4. Modification of nematocyst uptake by nudibranchs exposed to *Tautoglabrus adspersus* when collected from (A) Isles of Shoals and (B) Nubble. *Indicates significant differences, $P < 0.05$. Nematocyst types as in Figure 1.

Work should continue on the mechanism of selection (prey choice vs. active cellular selection by the nudibranch), variation in the types or proportions of nematocysts produced by the cnidarian prey in response to nudibranch predation, and differences in selective incorporation by other nudibranch species in the face of changing predation pressures.

The phenomenon of aeolid nudibranchs changing their defensive nematocyst regime may be widespread, though that has yet to be determined. Since the ability of a nudibranch to choose noxious organelles depends upon the variety of nematocysts available in the prey species, then the nudibranch's ability to respond to external cues is influenced by whether it is a specialist with a definite nematocyst array contained within its prey or a generalist capable of acquiring a wider range of nematocyst types from a variety of prey species. It may also be that large or potent nematocysts can only be incorporated at certain life-history stages due to physical limitations. Obviously the hydroid prey does not passively provide its defenses, and the nudibranch is not merely an adapted consumer that can choose from among an array of weapons without cost. The interaction is dynamic in its intricacies and malleable from the

perspective of both predator and prey. These concepts provide avenues of further study to elucidate the dynamics that control nematocyst uptake and the potential for predator response by aeolid nudibranchs. Determining how such predilection operates and its efficacy in deterring predation will help us better understand ecological communities and

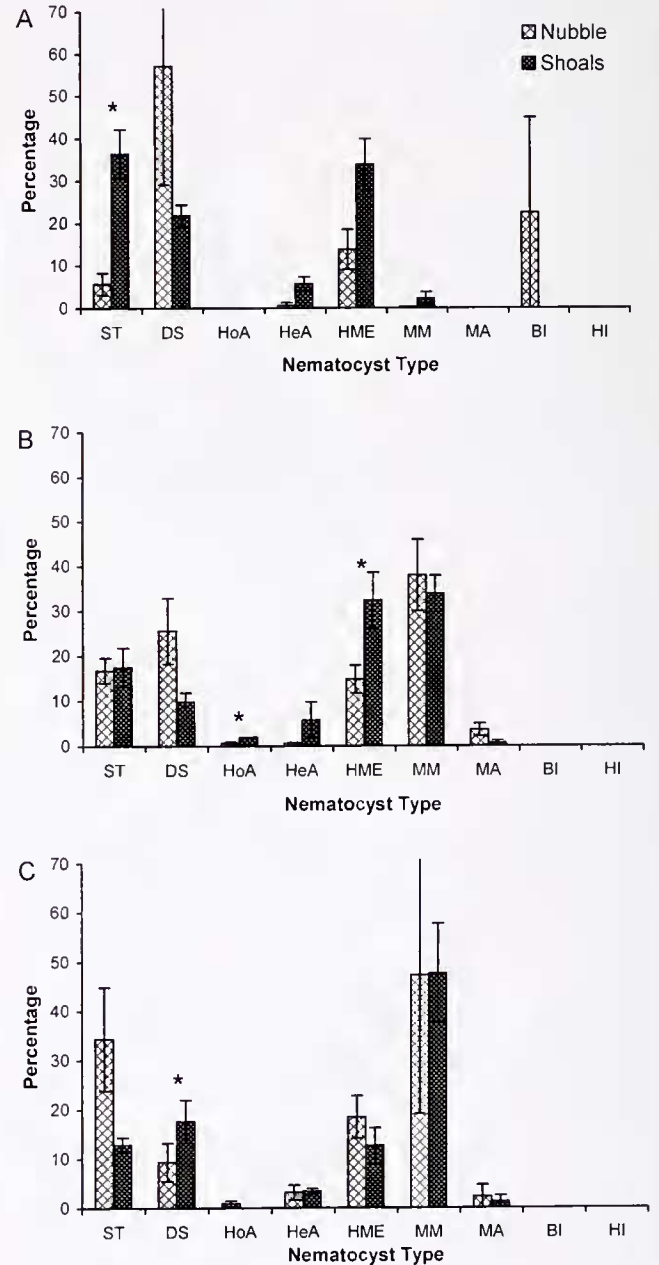


Figure 5. Comparison of control groups of *Flabellina verrucosa* collected from two sites in the southern Gulf of Maine. Results for each predator treatment are presented separately: (A) *Crossaster papposus*, (B) *Tautoglabrus adspersus*, and (C) *Carcinus maenas*. *Indicates significant differences, $P < 0.05$. Nematocyst types as in Figure 1.

the selective pressures that have brought about their formation.

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